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P.A. Chambers, E.E. Prepas,
M.L. Bothwell and H.R. Hamilton

Aquatic Ecology Division
National Hydrology Research Institute
Environment Canada
Saskatoon, Saskatchewan
S7N 3H5

**ROOTS VERSUS SHOOTS IN NUTRIENT UPTAKE
BY AQUATIC MACROPHYTES IN FLOWING WATERS**

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Roots versus Shoots in Nutrient Uptake by Aquatic Macrophytes in Flowing Waters

P. A. Chambers, and E. E. Prepas

Department of Zoology and Meenook Biological Research Station, University of Alberta, Edmonton, Alta. T6G 2E9

M. L. Bothwell

National Hydrology Research Institute, Saskatoon, Sask. S7N 3H5

and H. R. Hamilton

HydroQual Consultants Limited, Calgary, Alta. T2B 0K6

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Transplant experiments conducted in the South Saskatchewan River, Saskatchewan, Canada showed that the aquatic macrophyte, *Potamogeton crispus*, obtained most of its nutrients through the roots. When plants were grown in buckets containing high ($602 \mu\text{g}\cdot\text{g}^{-1}$ total phosphorus; $712 \mu\text{g}\cdot\text{g}^{-1}$ total organic nitrogen) or low ($258 \mu\text{g}\cdot\text{g}^{-1}$ total phosphorus; $109 \mu\text{g}\cdot\text{g}^{-1}$ total organic nitrogen) nutrient sediments and exposed to high ($75 \mu\text{g}\cdot\text{L}^{-1}$ soluble reactive phosphorus (SRP); $530 \mu\text{g}\cdot\text{L}^{-1}$ total dissolved nitrogen (TDN), or low ($10 \mu\text{g}\cdot\text{L}^{-1}$ SRP; $323 \mu\text{g}\cdot\text{L}^{-1}$ TDN) nutrient concentrations in the open water, biomass, shoot density and tissue nutrient concentrations were largely determined by sediment type, rather than open water chemistry. These results indicate that the roots are an important site of nutrient uptake for aquatic macrophytes in flowing waters.

Les expériences de transplantation faites dans la rivière South Saskatchewan en Saskatchewan, Canada, ont montré que la plante macrophyte aquatique, *Potamogeton crispus*, se procurait la plupart des substances nutritives dont elle a besoin grâce à ses racines. Lorsque des plantes étaient laissées à pousser dans des seaux contenant des sédiments riches ($602 \mu\text{g}\cdot\text{g}^{-1}$ en phosphore total; $712 \mu\text{g}\cdot\text{g}^{-1}$ en azote organique total) ou pauvres ($258 \mu\text{g}\cdot\text{g}^{-1}$ en phosphore total; $109 \mu\text{g}\cdot\text{g}^{-1}$ en azote organique total) en substances nutritives et qu'elles étaient exposées à des concentrations en substances nutritives élevées ($75 \mu\text{g}\cdot\text{L}^{-1}$ de phosphore réactif soluble, $530 \mu\text{g}\cdot\text{L}^{-1}$ d'azote dissous total) ou peu élevées ($10 \mu\text{g}\cdot\text{L}^{-1}$ de phosphore réactif soluble, $323 \mu\text{g}\cdot\text{L}^{-1}$ d'azote dissous total) dans l'eau non liée, on a constaté que la biomasse, la densité des pousses et la concentration en substances nutritives des tissus étaient largement déterminées par le type de sédiments plutôt que par la chimie de l'eau non liée. Ces résultats indiquent que les racines constituent un site important d'absorption des substances nutritives chez les plantes macrophytes aquatiques en eau courante.

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The role of sediments versus open water in supplying nutrients to aquatic macrophytes has long been debated, particularly with respect to the management of aquatic weeds and the control of lake eutrophication (Hutchinson 1975; Best and Mantai 1978; Carignan and Kalff 1980; Agami and Waisel 1986). Several studies have clearly demonstrated that the sediments are the major source of phosphorus and nitrogen for rooted aquatic plants growing in lakes (Nichols and Keeney 1976a,b; Best and Mantai 1978; Carignan and Kalff 1980; Barko and Smart 1980, 1981; Smith and Adams 1986). However, for aquatic macrophytes growing in flowing waters, the nutrient source has yet to be quantified. The observation that the bottom sediments of many rivers are too coarse to represent a significant nutrient pool and that flowing water provides a continuous supply of nutrients and prevents localized patches of nutrient depletion around the shoot has led to the assumption that aquatic macrophytes in rivers obtain most of their nutrients

from the open water. Nevertheless, studies on flowing waters have failed to demonstrate any correlation between open-water nutrient concentrations and aquatic macrophyte biomass or tissue nutrient concentrations (Owens and Edwards 1961; Ladle and Casey 1971; Kern-Hanson and Dawson 1981; Blachford and Ongley 1984). This inconsistency has been attributed to the presence of growth-limiting factors other than nutrients (Kern-Hanson and Dawson 1981) or open-water nutrients in excess of the plants' requirements (Owens and Edwards 1961; Blachford and Ongley 1984). However, the possibility remains that aquatic weeds in flowing waters are obtaining their nutrients from the bottom sediments.

The aim of our study was to determine the role of roots versus shoots in nutrient uptake by aquatic angiosperms in flowing waters. In many rivers on the North American prairies, increased nutrient loading (due to sewage, agricultural and/or industrial inputs) and water withdrawal (for irrigation, munic-

ipal, and industrial requirements) have been associated with an abundant growth of aquatic plants (Tones et al. 1980; Blachford and Ongley 1984; Charlton et al. 1986). As a first step towards establishing cost-efficient guidelines for nutrient loading so as to reduce aquatic macrophyte growth, the source of nutrients utilized by aquatic plants in rivers must be established. The approach we adopted was a transplant experiment, conducted in the South Saskatchewan River, Saskatchewan, Canada. *Potamogeton crispus* L. was grown in pails containing natural sediments with different levels of nitrogen and phosphorus, at two sites with very different concentrations of nitrogen and phosphorus in the open water. The effects of variations in sediment to water phosphorus and nitrogen ratios could therefore be examined in relation to plant growth and nutrient uptake.

Materials and Methods

Study Site

The South Saskatchewan River is a seventh-order stream and a major tributary of the Saskatchewan-Nelson river system. It originates in south-eastern Alberta, Canada with the convergence of the Bow and Oldman rivers and flows north-east across Saskatchewan, joining with the North Saskatchewan River east of Prince Albert, Saskatchewan to form the Saskatchewan River. The latter flows into Cedar Lake and then Lake Winnipeg, eventually draining into Hudson Bay through the Nelson River. Throughout much of the South Saskatchewan River, flows are regulated by the Gardiner Dam located 114 km upstream of Saskatoon. Operating guidelines for the dam require that a minimum flow of $42.5 \text{ m}^3 \cdot \text{s}^{-1}$ be maintained in the river at Saskatoon. During the past 10 yr, mean monthly flows (May – September) at Saskatoon averaged $121 \text{ m}^3 \cdot \text{s}^{-1}$.

Sewage from the City of Saskatoon has been discharged into the South Saskatchewan River for over 75 yr and represents the major source of nutrients to the river (Tones et al. 1980). Water quality assessments during the past 20 yr have documented increased nitrogen and phosphorus concentrations, and increased macrophytic and periphytic growth downstream of the Saskatoon sewage treatment plant outfall (Tones et al. 1980; Kerc 1986). As much as 80% of the total phosphorus (TP) and 50% of the total Kjeldahl nitrogen (TKN) loads in the open water downstream of Saskatoon are due to the sewage effluent, with summer (July–September) TP and TKN loads from the sewage treatment plant averaging 416.7 and $2062.5 \text{ kg} \cdot \text{d}^{-1}$, respectively, over 2 yr (1984–85) (Kerc 1986). By comparison, TP and TKN loads in the open water upstream of the sewage treatment plant averaged 96.9 and $1595.1 \text{ kg} \cdot \text{d}^{-1}$ over the same period.

Our study site was located 22 km downstream of the sewage treatment plant. Here, open-water nutrient concentrations and aquatic macrophyte growth along the East riverbank were considerably less than along the West bank as a result of limited mixing between the plume of wastewater effluent from the sewage treatment plant (located on the West bank) and the river water.

Experimental Design

Potamogeton crispus was collected from the South Saskatchewan River on June 28, 1987. Intact rhizomes bearing two to three stems (each <8 cm long) were planted in 2-L plastic pails containing homogenized river sediments which had been collected with a shovel from either 15 km upstream or 22 km

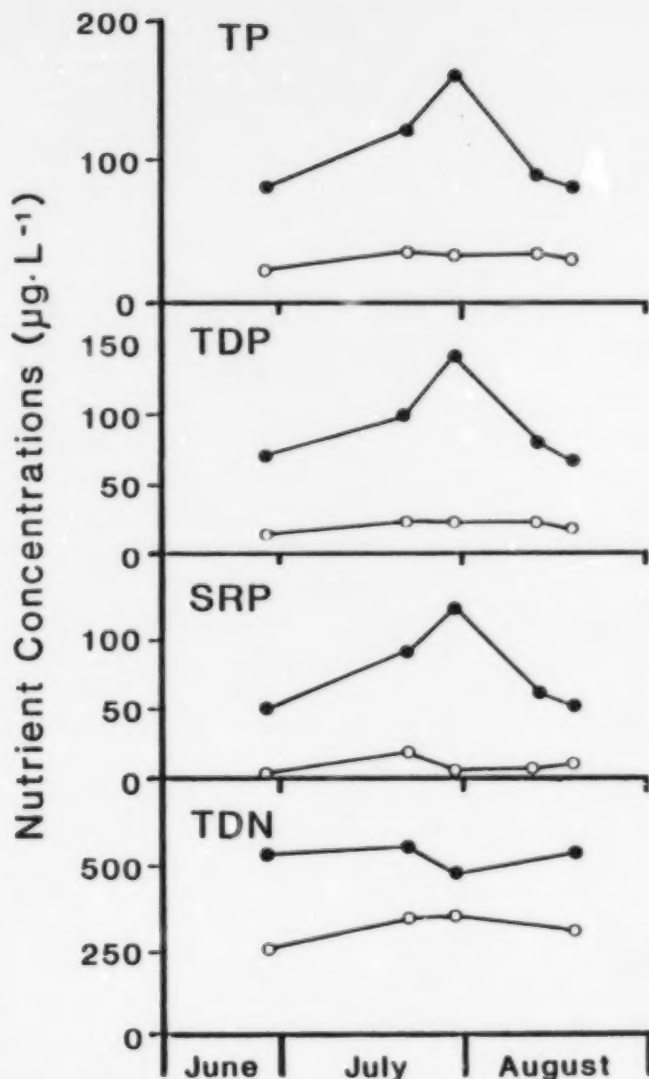


FIG. 1. Open-water total phosphorus (TP), total dissolved phosphorus (TDP), soluble reactive phosphorus (SRP), and total dissolved nitrogen (TDN) concentrations in the South Saskatchewan River, 22 km downstream of the Saskatoon sewage treatment plant, during the transplant experiment: (●) West bank; (○) East bank.

downstream (West bank) of the Saskatoon sewage treatment plant. The sediments were packed firmly into the pails such that nutrient exchange between the sediment-bound or pore-water pools and the open water was likely minimal. The experimental treatments followed a factorial design whereby replicate buckets (six) of each sediment type (high or low) were placed at a depth of 0.6 m in the river at sites with high or low nutrient concentrations in the open water (i.e. the West and East banks, 22 km downstream of the Saskatoon sewage treatment plant). After 7 wk, plants were harvested, separated into shoot, root, and rhizome, and dried at 110°C to constant weight. Shoot density was determined as the number of stems per pail. Total phosphorus and total organic nitrogen in plant shoots and sediments (collected prior to planting) were extracted by wet oxidation with sulphuric acid and hydrogen peroxide (Parkinson and Allen 1975) and analyzed spectrophotometrically by the phenol-hypochlorite (Hasenmore and Rouphan 1976) or molyb-

TABLE 1. Physical and chemical parameters of the open water along the West and East banks of the South Saskatchewan River, collected 22 km downstream of the Saskatoon sewage treatment plant on August 19, 1987.

	West bank	East bank
pH	8.26	8.62
Conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$)	445	425
Alkalinity ($\text{mg CaCO}_3\cdot\text{L}^{-1}$)	150	146
Hardness (total as CaCO_3)	176.7	172.8
Total dissolved solids ($\text{mg}\cdot\text{L}^{-1}$)	253	245
Ions ($\mu\text{g}\cdot\text{L}^{-1}$)		
Bicarbonate	182.9	165.4
Calcium	43.4	42.0
Chloride	8.8	6.9
Magnesium	16.6	16.5
Potassium	2.73	2.49
Sodium	23.6	22.5
Sulphate	67.9	66.7

denim blue (Stainton et al. 1977) colorimetric methods, respectively. Exchangeable phosphorus was extracted from fresh sediment by shaking for 16 h with 0.1N NaOH-NaCl and measured spectrophotometrically (Stainton et al. 1977). Sediment organic content was measured as loss after ignition at 550°C for 5 h. Sediment water content was measured as loss after drying at 110°C to constant weight. All sediment and tissue analyses were performed in triplicate.

Surface water temperature was measured and surface water samples were collected for phosphorus (total (TP), total dissolved (TDP), and soluble reactive (SRP) phosphorus) and total dissolved nitrogen (TDN) along both river banks every 2–3 wk throughout the experiment. On one occasion (August 19), water samples were also analyzed for pH, conductivity, hardness, alkalinity, total dissolved solids, and dominant ion concentrations. All water chemistry was performed by the Western Regional Water Quality Branch Laboratory, Environment Canada, Saskatoon, using procedures outlined in their manual (Environment Canada 1979). Current velocity and underwater penetration of photosynthetically active radiation (PAR) were measured at each site on three occasions with a Gurly-Price model 22 current meter or a LiCor quantum radiometer, respectively. The vertical attenuation coefficient for PAR (K) was calculated by linear regression from the Beer-Lambert equation.

Data were analyzed with the Statistical Analysis System (SAS Institute Inc. 1982). The response of plant biomass, shoot density, and tissue nutrient levels to variations in sediment type and water quality were determined by analysis of variance, followed by least significant difference multiple comparison of means tests. To stabilize variance, a logarithmic transformation was applied to the biomass and shoot density data.

Results

Environmental Conditions

Phosphorus and nitrogen concentrations in the open water were consistently greater along the West than the East bank for all sampling dates (Fig. 1). Phosphorus concentrations along the West bank increased in late July. Total dissolved nitrogen concentrations, however, remained relatively constant throughout the study. Conductivity, alkalinity, hardness, total dissolved solids, and dominant ion concentrations in the open water were also greater along the West than the East bank

(Table 1). These differences were, however, slight as compared with differences in nitrogen and phosphorus levels between the two banks.

Comparison of initial nutrient concentrations, organic matter, and water content in the South Saskatchewan River sediments showed that sediments from downstream of Saskatoon were more fertile than those from upstream (Table 2). The upstream sediments also appeared coarse and sandy as compared with the finer-particle sediments from downstream. The range in sediment phosphorus concentrations we observed was similar to that determined for natural sediments collected from other Canadian prairie river systems (P. A. Chambers, unpubl. data; Cross et al. 1986). Our upstream sediments will henceforth be referred to as low nutrient sediments as compared with the high nutrient downstream sediments.

Attenuation of underwater PAR showed little variation between sampling dates. There was, however, a significant but weak ($0.01 < P < 0.05$) difference between the two riverbanks, with attenuation coefficients of 0.79 ± 0.05 and $1.04 \pm 0.06 \text{ m}^{-1}$ (mean $\pm 1 \text{ SE}$) for the East and West banks, respectively. As the natural plant community colonized the entire riverbed (2 m maximum depth), it is unlikely that plant growth was light-limited at our 0.6 m deep study sites.

Temperature ranged from 16 to 26°C over the study period and did not differ between the East and West banks. Current velocity, measured 0.1 m below the water surface, was $22.9 \text{ cm}\cdot\text{s}^{-1}$ along both banks on June 28 and decreased to $11.9 \text{ cm}\cdot\text{s}^{-1}$ by August 19, presumably due to the increased biomass of aquatic weeds which blocked current flow.

Plant Growth

Biomass (total, shoot, root and rhizome) and shoot density of *P. crispus* were consistently greater ($P < 0.01$) in high than in low nutrient sediments (Table 3). Analysis of variance showed that while plant biomass and density were highly dependent upon sediment type ($P < 0.001$), there was no significant response to water phosphorus and nitrogen levels ($P > 0.25$). There was also no significant interaction between open-water and sediment nutrient treatments ($P > 0.75$). On an areal basis, shoot biomass in the low nutrient sediments was approximately $19 \text{ g dry weight}\cdot\text{m}^{-2}$ compared with $86 \text{ g dry weight}\cdot\text{m}^{-2}$ in the high nutrient sediments.

Tissue nitrogen and phosphorus concentrations for *P. crispus* were also consistently greater ($P < 0.0001$) in the high than in the low nutrient sediments (Table 4). However, unlike biomass and shoot density which were independent of water quality, tissue phosphorus levels and nitrogen:phosphorus (N/P) ratios showed a significant, but weak, response to water quality. Thus, in low nutrient sediments, tissue phosphorus concentrations were greater ($0.01 < P < 0.05$) and N/P ratios were lower ($0.0001 < P < 0.001$) for plants exposed to nutrient-enriched river water. There was no significant difference ($P > 0.05$) in tissue phosphorus concentrations or N/P ratios for plants growing in high nutrient sediments in either high or low open-water nutrient concentrations.

Discussion

Biomass and shoot density of *P. crispus* were primarily determined by sediment type and not significantly affected ($P > 0.25$) by open-water nutrient concentrations. Thus, plants growing in low nutrient sediments had consistently less biomass

TABLE 2. Chemistry of sediments, collected from the South Saskatchewan River upstream and downstream of Saskatoon, at the start of the transplant experiment (mean $\pm$ 1 SE).

	Upstream	Downstream
Total phosphorus ($\mu\text{g} \cdot \text{g}^{-1}$ dry weight)	258 $\pm$ 26	602 $\pm$ 9.0
Exchangeable phosphorus ($\mu\text{g} \cdot \text{g}^{-1}$ dry weight)	11.3 $\pm$ 1.0	89.0 $\pm$ 3.7
Total organic nitrogen ($\mu\text{g} \cdot \text{g}^{-1}$ dry weight)	109 $\pm$ 4.0	712 $\pm$ 9.0
Percent water content	20.3 $\pm$ 0.5	30.4 $\pm$ 0.1
Percent organic matter	0.48 $\pm$ 0.07	2.40 $\pm$ 0.04

TABLE 3. Biomass ($\text{g dry weight} \cdot \text{pail}^{-1}$) and shoot density of *P. crispus* grown in high or low nutrient sediments at sites with high or low concentrations of nitrogen and phosphorus in the open water. Data were back-transformed after $\log(X+1)$ transformation. For any parameter, values sharing the same superscript are not significantly different ($P > 0.05$; $n = 6$).

Open-water nutrients	Sediment nutrients	Biomass				Shoot density
		Total	Shoot	Root	Rhizome	
Low	High	1.67 ^a	1.20 ^a	0.27 ^a	0.18 ^a	60 ^a
	Low	0.29 ^b	0.19 ^b	0.05 ^b	0.05 ^b	13 ^b
High	High	1.83 ^a	1.38 ^a	0.20 ^a	0.17 ^a	47 ^a
	Low	0.38 ^b	0.25 ^b	0.04 ^b	0.03 ^b	12 ^b

TABLE 4. Tissue phosphorus (P) and nitrogen (N) concentrations ($\text{mg} \cdot \text{g}^{-1}$ dry weight; mean $\pm$ 1 SE; $n = 6$) for *P. crispus* grown in high or low nutrient sediments at sites with high or low concentrations of nitrogen and phosphorus in the open water. For any parameter, values sharing the same superscript are not significantly different ($P > 0.05$).

Open-water nutrients	Sediment nutrients	Tissue Nutrient Concentrations		
		P	N	N/P
Low	High	3.77 $\pm$ 0.11 ^a	36.05 $\pm$ 1.55 ^b	9.57 $\pm$ 0.32 ^a
	Low	1.82 $\pm$ 0.12	24.74 $\pm$ 1.20 ^a	13.68 $\pm$ 0.40
High	High	3.88 $\pm$ 0.20 ^a	31.66 $\pm$ 1.30 ^b	8.27 $\pm$ 0.58 ^a
	Low	2.50 $\pm$ 0.21	26.81 $\pm$ 1.06 ^a	10.87 $\pm$ 0.48

and fewer shoots than ones growing in high nutrient sediments. Tissue nutrient concentrations were also largely determined by sediment type. However, tissue phosphorus levels and N/P ratios also showed a significant, but weak, correlation with open-water nutrient concentrations, such that plants growing in low nutrient sediments had higher tissue phosphorus levels and lower N/P ratios when exposed to phosphorus-rich river water.

Our results indicate that nutrient uptake by aquatic macrophytes in the South Saskatchewan River is largely effected by the roots. Studies on European streams and rivers have shown that aquatic macrophyte biomass and tissue nutrient concentrations are not correlated with open-water nutrient concentrations (Owens and Edwards 1961; Ladle and Casey 1971), which is consistent with our observation on the importance of sediment nutrients to the growth of rooted aquatic plants in flowing waters. However, Kern-Hanson and Dawson (1981) observed that for 19 streams in Denmark, aquatic macrophyte biomass and tissue nutrient concentrations were not correlated with either open-water or sediment nutrient concentrations, suggesting that in these streams factors other than nutrients limited growth.

The importance of sediment type in the control of riverine plant growth is consistent with results of nutrient uptake studies on aquatic macrophytes in lakes. Carignan and Kalff (1980) demonstrated that over 70% of total plant phosphorus is derived from the sediments for aquatic angiosperms grown in nonflowing waters with TP concentrations in the open water ranging

from 10 to 290 $\mu\text{g} \cdot \text{L}^{-1}$. Other investigators (Best and Mantai 1978; Barko and Smart 1980; Smith and Adams 1986) have also observed that phosphorus uptake by roots exceeds that by shoots in nature. While the roots of submersed aquatic plants are also capable of nitrogen uptake (Nichols and Keeney 1976a,b; Best and Mantai 1978), the relative contribution of shoots versus roots to nitrogen uptake for aquatic macrophytes in lakes is more equivocal (Agami and Waisel 1986).

In summary, our results showed that *P. crispus*, one of the dominant aquatic macrophytes in the South Saskatchewan River, obtained most of its nutrients through the roots. While further experiments are needed to extend this conclusion to other flowing waters, the generality of our results is supported by our experimental design in which only sediment and open-water nutrient levels varied and other factors likely to affect plant growth (i.e. irradiance, current velocity, temperature, river water-porewater exchange) remained constant. At present, however, the results do not allow any conclusion as to whether the nutrients taken up by the roots are derived from a sediment-bound pool or river water as it passes through coarse-grain sediments. Since increased current velocity results in river beds with larger sediment particles which are usually less nutrient rich and less densely packed, the proportion of river water to sediment-bound nutrients in the rooting zone will depend upon flow rate. Our finding on the importance of root uptake for riverine macrophyte nutrition has important implications for aquatic weed control, suggesting that the impact of decreased nutrient loading on aquatic macrophyte growth will depend upon nutrient availability and particle size of the river bed sediments.

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